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Salientia Morphology

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Introduction

Salientia is a superorder of lissamphibians, which includes frogs and toads (order Anura) and the Early Triassic Proanura *Triadobatrachus* and *Czatkobatrachus* (Benton 2015). This is the major extant order of the class Amphibia, encompassing more than 7000 species (Frost 2019) with a high morphological diversity. They are distributed all around the globe, except for the poles and most oceanic islands. Salientia synapomorphies (characteristics that are shared by the group, derived from a common ancestral) include: lack of a tail in the adult stage; five to nine presacral vertebrae; postsacral vertebrae (posterior to the pelvis) fused into a bony coccyx; and hind limbs elongated, modified for jumping. Other characteristics of Salientia include: fertilization, often external; eggs laid in water or humid places; aquatic larval stage present in most species; males usually with vocal cords, vocal sac, and a voice (Hickman et al. 2014; Kardong 2015). In this section, we synthesize the main knowledge about larval and adult morphologies, and also include changes during metamorphosis, adult sexual dimorphism, and evolution.

Larval Morphology

Most Salientia species have an aquatic, free-swimming larval stage (tadpole). Tadpoles are typically found in ponds and streams, but some species grow in puddles, roadside ditches, or even in the ground litter. They mainly feed by scrapping off the substrate or capturing particles suspended in the water, though there are some predator species. These specialized habits require an entirely different morphology from the adult. Anuran adults have short bodies with long limbs and are tailless, while tadpoles have a tail with fins and are limbless during early stages of development (Fig. 1). Skin, mouthparts, digestive (usually herbivore larvae and predator adult), and respiratory systems (aquatic larvae and air breathing adult) are also dramatically different.

The mouthparts are composed of an oral disk, usually covered with papillae (small dermal projections), several corneous denticles (toothlike projections) arranged in rows, and two strong, highly keratinized, corneous beaks. This arrangement is highly variable according the food habits of the species: tadpoles that scrape stones and other hard substrates usually have more corneous

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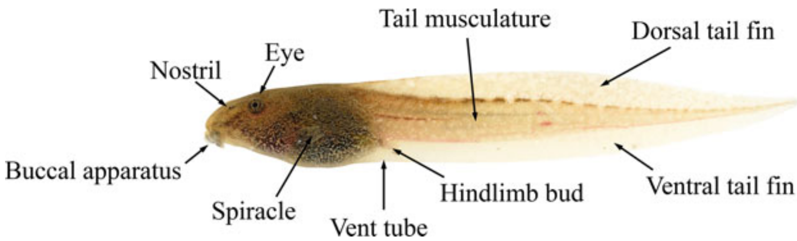


Salientia Morphology, Fig. 1 General morphology of a tadpole

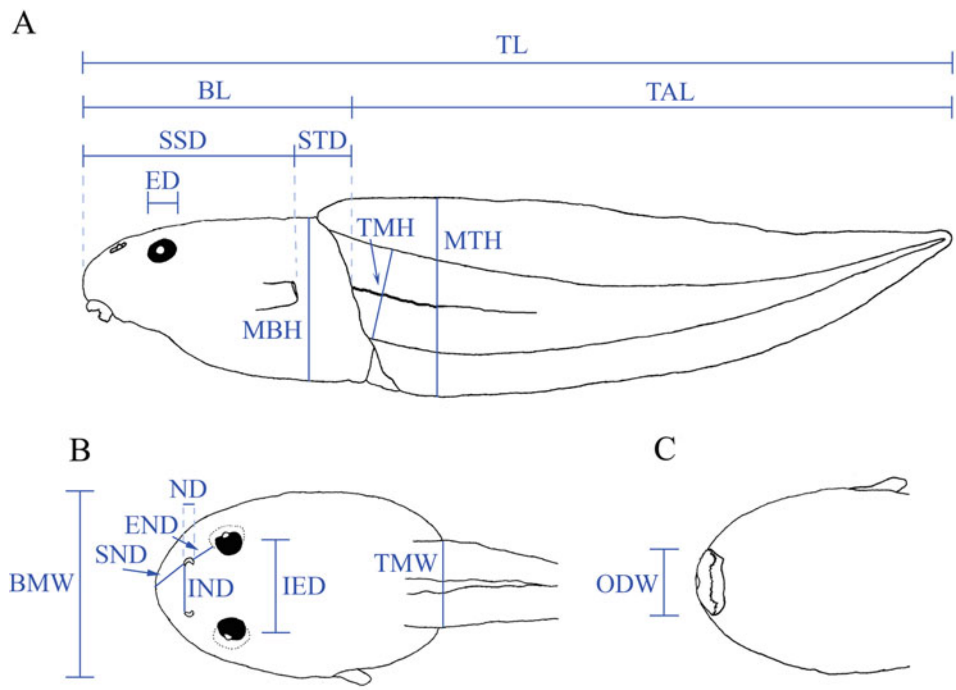
denticles, while predators have reduced oral discs without denticles, but stronger corneous beaks. The position of the mouthparts also reflects food habits: species that feed on deposited particles have anteroventrally oriented mouthparts; species that feed on suspended particles or that are predators have anteriorly oriented mouthparts; species that feed on particles in the water surface have a dorsally oriented funnel-shaped oral disk. Recent studies have also shown a large diversity of internal oral morphology across species.

Besides the variation on mouthparts, the overall morphology varies according to species habits. The tadpoles of pond breeders characteristically have large bodies and deep caudal (tail) fins, which in some species might have a terminal tail extension, like the familiar swordtail fishes (*Xiphophorus*). The mouth is relatively small, located anteriorly, on the underside or upperside of the snout and usually contains weak denticles. These tadpoles swim easily in quiet waters and feed on attached and free-floating vegetation, including algae. In contrast, the stream tadpoles have depressed bodies, long muscular tails, and shallow caudal fins. The mouth is relatively large and usually contains many rows of strong denticles. In highly modified stream tadpoles, the mouth is ventral and modified as an oral sucker, with which the tadpole anchors itself to stones. These tadpoles swim slowly, grazing on the coating of bacteria and algae as they move.

As underwater breathers, tadpoles are lungless and perform branchial respiration. The gills are external in the early stages of development, eventually becoming internalized in branchial chambers or gill cavities due the development of the opercula (gill covering). The water is pumped through the mouth and pharynx to the gill cavity by muscular contractions. After irrigating the gills, the water is expelled through one or two spiracles (small slit- or tube-like openings), depending on the species. Most species have a single spiracle located on the left side of the body. Others possess a single ventrally positioned spiracle, or two spiracles, one on each side of the body.

In taxonomic studies, tadpole descriptions usually address all of these external features plus others, like eye color and position, nostrils shape and position, vent-tube position (the opening of the cloaca), tail and fin sizes and proportions, body and tail coloration, and presence or absence of neuromasts (mechanical sensors that compose the lateral line). Morphometrically, the following measurements are usually present (Fig. 2): total length (TL), body length (BL), body width (BW), body height (BH), oral disc width (ODW), snout–spiracle distance (SSD), snout–nostril distance (SND), nostril diameter (ND), inter–nostril distance (IND), eye–nostril distance (END), eye diameter (ED), inter–eye distance (IED), spiracle–tail distance (STD), tail length (TL), tail muscle height (TMH), tail muscle width (TMW), and maximum tail height (MTH). In order to enable comparisons between tadpoles with similar development, Gosner (1960) established a table for classifying the development from the one-cell egg (stage 1) to a completely metamorphosed anuran (stage 46).

Tadpoles have a cartilaginous skeleton, divided in a chondrocranium and hyobranchial, axial, and appendicular skeletons. The chondrocranium is a case that houses and protects the brain and main sensory organs, besides supporting the feeding system. The hyobranchial skeleton provides support and directs current water to the gills. The axial skeleton is composed by the vertebral column and is responsible for sustaining tail muscles, playing a fundamental role on under the water mobility. The appendicular skeletons are absent through



Salientia Morphology, Fig. 2 Schematic drawing of measurements usually presented in tadpole descriptions. (**a**) lateral view; (**b**) dorsal view; (**c**) ventral view. See text for abbreviatures

most of the tadpole's development, appearing only during metamorphosis (Altig and McDiarmid 1999).

Metamorphosis

After a variable period of growth, the tadpole undergoes metamorphosis, in which limbs become well developed, and the tail is lost, two of the most obvious morphological changes that take place. Such changes occur gradually throughout tadpole development, the tail loss being one of the last morphological changes. Among the first changes is the appearance of hind limb buds, which grow and develop until completely differentiating into hind limbs with toes, webbing, and tubercles (small, round nodules). Larval mouth parts begin to change; the corneous denticles and papillae, if present, disappear, while the jaws and true teeth develop. A tongue (except in pipids) and associated hyolaryngeal structures develop. The eyes are enlarged and undergo structural modifications; eyelids develop. Later on, the forelimbs emerge through the operculum skin; the tail begins to shrink, being resorbed by the body and the skin thickens following development of dermal glands. The vertebral column and limb bones ossify (a process that continues during the entire adult life of the anuran), and the adult digestive system differentiates as the long coiled intestine shrinks into at short, thick-walled, folded intestine. The lungs develop, and, for a short period of time, tadpoles have both lungs and gills, before the latter disappear.

How, when and where the changes from larva to adult take place varies greatly across species – a fascinating aspect of studying frogs. The time it takes before metamorphosis depends on the species but also on environmental conditions like temperature and food availability. Most tadpoles complete their development in 2 or 3 months, but there are notable exceptions. Tadpoles of spadefoot toads, genus *Scaphiopus*, develop in temporary rain pools in arid parts of North America, where it is imperative for the tadpoles to complete their development before the pools dry up. Some *Scaphiopus* tadpoles metamorphose about 2 weeks after hatching. In its turn, tadpoles of the neotropical tree frog *Flectonotus pygmaeus* have the intestines filled with yolk and do not feed until the metamorphosis is complete. They are carried in a female dorsal pouch and metamorphosis is completed in 11–17 days after being released from the pouch and 34–43 days after mating (Duellman et al. 2011). Contrastingly, in the northern part of its range in North America, the tadpoles of the bullfrog *Lithobates catesbeianus* require 3 years to undergo their development.

Adult Morphology

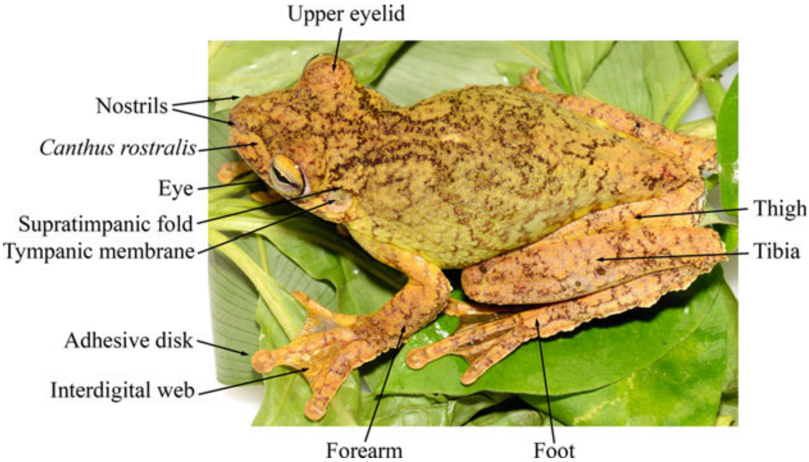
The name "Salientia" means "leapers." Not surprisingly, anurans are animals built for jumping, and many of their body features are adapted for this type of locomotion. The short, flattened body provides mid-air stability. Jumping relies on simultaneous movement of hind legs, which are much larger than the front legs, acting as a spring together with the pelvic girdle. The muscles of the hind legs act as a power output generated during a frog's jump and is enhanced by elastic energy stored in tendons and muscle fibers. The relative size of each toe ensures that all of them will be in contact with the ground during the impulse, increasing friction. Anurans have completely lost their tail and the vertebral column is greatly shortened through reduction in number of vertebrae. The scapular girdle is strongly attached to the column by cartilage ligaments, absorbing the impact on the arms during landing. Bony elements and teeth are reduced in most species, which presumably serves to reduce the mass of the skull, thereby enhancing jumping performance (Vitt and Caldwell 2013).

Besides jump, anurans might have other modes of locomotion. A few frogs have become almost entirely aquatic and typically have streamlined bodies, large, muscular hind legs, and hind feet with webbing extending to the tips of the toes. Often anurans can burrow in loose soil or sand to escape cold winters, hot summers, or long dry seasons. Such frogs dig with the hind feet, which are often equipped with special tubercles. Their hind legs are relatively short, with the tibio-fibula especially shortened. Tree frogs have adhesive discs on the fingertips, allowing them to adhere to some suspended surface during the jump. Gliding frogs typically have very large toe pads and extensive webbing on both the front and hind feet, and some have skin flaps on the sides of the body and legs. These frogs spread their toes and hold their limbs bent to the sides of the body while gliding, reducing the landing speed and allowing for a longer jump.

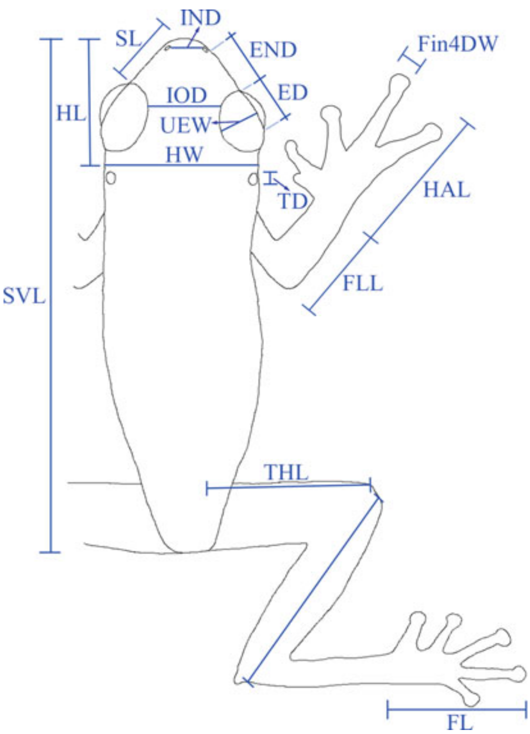
External Morphology

Although most Salientia species are readily recognizable by their external morphology (Fig. 3), there is a great variety of sizes and structural modifications. Many frogs are tiny animals; perhaps one of the smallest adults is the Brazilian *Brachycephalus sulfuratus*, with 8.0 mm or less in total body length, whereas the West African goliath frog, *Conraua goliath*, has a body length of nearly 300 mm. Morphometric measurements are necessary for species delineation, phylogenetic analyses, and even our understanding of evolutionary change in an organism's physical characteristics. In a recent review of morphometric measurements for anurans (Watters et al. 2016), a subset of 16 measurements were recommended as relevant to frogs' descriptions (Fig. 4). These are: head width (HW), snout–vent length (SVL), tibia length (TL), interorbital distance (IOD), head length (HL), eye diameter (ED), internarial distance (IND), eye–nostril distance (EN), foot length (FL), tympanum diameter (TD), thigh length (THL), snout length (SL), hand length (HAL), forearm length (FLL), upper eyelid width (UEW), and Finger IV disk width (Fin4DW). However, frogs continue to grow throughout their life. Thus proportions, rather than actual measurements, are better for comparing samples and species and can be expressed as ratios of between a specific measurement and the SVL.

The shape of the snout is a reliable and easily discernible taxonomic feature. In dorsal view, the snout can be semicircular, nearly rounded, rounded, subovoid, subelliptical, pointed, truncate,



Salientia Morphology, Fig. 3 General morphology of an adult amphibian



Salientia Morphology, Fig. 4 Schematic drawing of measurements recommended for anuran descriptions. See text for abbreviatures

or mucronate; these same shapes are evident in lateral views, although laterally, the snouts of some species are rounded, vertical, obtuse, acute, strongly acute, acuminate or protruding (see Heyer et al. 1990 for more information). Still on the anterior part of the head, two highly subjective characters are present: *canthus rostralis*, the angle of the head from the anterior corner of the eye to the nostrils or to the tip of the snout; and, loreal region, the side of the face between the *canthus rostralis* and the lips. A tympanum and usually a tympanic ring are evident in most species. Commonly, a supratympanic (dermal) fold extends posteriorly from the corner of the eye and passes just above the tympanum and continues onto the flank, sloping downward to a point above the insertion of the arm.

Some characters are found in anuran eyes, such as pupil orientation and presence of pigment on the palpebral membrane. Although the most common orientation is horizontal, some species have vertical pupils. The palpebral membrane is usually transparent (unpigmented) or only slightly pigmented in most species, with rare cases of pigmented reticulation. Also, palpebral and rostral (on the tip of the snout) fleshy appendages might be present in some species, as some of the genus *Proceratophrys* and *Hemiphractus*. In males of many species of frogs, vocal sacs connect to the buccal cavity, typically via slit-like openings, and are inflated during vocalization. Their morphology varies from a median single subgular sac, to bilobate and paired subgular sacs, or to paired lateral sacs.

Structural characters of the hands and feet are of immense taxonomic importance. Alberch and Gale (1985) recognized anuran fingers as homologous to vertebrate digits II–V. The relative lengths of the digits and toes, from shortest to longest, are usually represented in scientific works. Some fighting males have a curved, sharp prepollical spine on each hand, anteriorly to Digit II. This structure was thought to be homologous of Digit I, but this idea is no longer accepted. On its ventral surface, both hands and feet might have tubercles, which are classified according to their position, shape, and quantity. Subarticular tubercles are those below the articulations of the phalanges. Supernumerary tubercles are the small ones on the ventral surfaces of the digits, adjacent to the larger subarticular tubercles. Inner metacarpal or metatarsal tubercles are the large tubercles on the ventral surface of the hand or foot, at the base of the shortest finger or toe, respectively. Outer metacarpal or metatarsal tubercles are the small tubercles on the ventral surface of the hand or foot at the base longest finger or toe, respectively. Tubercles might be absent in many species.

Fingers and toes might have an interdigital webbing: a membranous skin that connects them with each other. The presence and extent of webbing on fingers and toes has been emphasized by many authors as a feature for recognition of different species, but it might exhibit considerable intraspecific variation, reducing its reliability for diagnosis. The degree of webbing is expressed in terms of how many segments of the digits (phalanges), hand (distal metacarpal), or foot (distal metatarsal) are free of webbing (see Myers and Duellman 1982; Savage and Heyer 1997 for more explanation).

The skin is the cellular boundary between animal and external environment. It serves as a protective barrier, preventing the invasion of microbes and inhibiting access by potential parasites, resists mechanical invasion and abrasion, and buffers the internal environment from extreme external conditions. The skin also acts in physiological regulation, sensory detection, respiration, and coloration. Several types of epidermal glands are widespread on the head, body, and limbs (mucous and poison glands are always present). The secretions produced by these glands include numerous polypeptides with several activities reported, including antibiotic, antitumor, and insulin-releasing activities. The skin is shed in a cyclic pattern of several days to a few weeks. Using its limbs, the frog emerges from the old skin, which is often consumed.

The color of amphibians is affected by the presence of pigmented cells (chromatophores) in the dermal layer of the skin. The three classes of chromatophores (melanophores, iridophores, and xanthophores) are arranged as a unit and produce the external coloration. Different classes can be combined and arranged to produce a wide range of colors and patterns. In some species, skin color can be quickly altered, in less than a minute, through dispersal or reduction of the eumelanin within the melanophores' processes.

Internal Morphology

When the first tetrapods colonized the earth, new demands affected their bodily systems. Supporting body weight and moving on the ground, capturing and ingesting food, breathing and mating were challenges to overcome. The musculoskeletal system was, perhaps, the most affected in this transition. The Salientia, of course, inherited morphological solutions for these challenges and adapted them for their own specialized way of life.

The anuran skeleton is highly specialized. The cranium, much different from other vertebrates, is light, flattened, scarcely ossified and with a small number of bones. Nevertheless, it is resilient enough to withstand the impact of the landing after a jump. The teeth are bicuspid and pedicellate (supported on a pedicel). The vertebral column is very short, with only five to nine presacral vertebrae, without ribs but with overlapping processes that reduce lateral movement. The postsacral vertebrae are fused in a long, single bone, the urostyle. Both scapular and pelvic girdles are firmly attached to the vertebral column, a characteristic inherited from the first tetrapods but enhanced by the jumper habit. The posterior limbs are longer than the anterior ones. Both fingers and toes have long and numerous articulated elements (with up to four phalanges), enhancing ability to grab and climb while helping with their ability to jump.

The cranial musculature contains one functional group for jaw movement and another for breathing and swallowing. The jaw muscles are attached to the dorsal, lateral, and ventral surfaces of the mandible to open and close the mouth. The muscles that function in respiration and swallowing move and support the gills and/or the hyoid and the tongue. The tongue is strong, muscular, retractile, and has a free posterior end. This end is highly glandular and produces a mucus that adheres to the prey, pulling it into the mouth. Thanks to *retractor bulbi* and *levator bulbi* muscles (the latter, a synapomorphy of Lissamphibia) and to the lack of a hard palate, the eyeballs can be pulled into the oral cavity, helping to swallow. The musculature of the vertebral column consists of epaxial (dorsal trunk) muscles and hypaxial (flank or ventral trunk) muscles providing rigidity and strength to the vertebral column and supporting the viscera, respectively. The pectoral girdle is anchored to the trunk vertebrae by axial muscles and absorbs the jump impact. The pelvic girdle has a less extensive muscular system. The limb muscles are divided into a dorsal extensor and a ventral flexor unit, both strong and robust.

Other systems differ less from the basic patterns found in vertebrates. The central nervous system includes the brain and the spinal cord. The brain is divided during development by a flexure into the forebrain and hindbrain, which are further partitioned, structurally and functionally. The forebrain consists of the telencephalon and the diencephalon and the midbrain consists of the mesencephalon and the hindbrain. Twelve pairs of cranial nerves arise from the brain. The spinal cord is a flattened cylinder of nerve cells that extends caudal through the vertebrae. Regarding the sensory system, two characteristics need to be mentioned: the presence of green rods on the eyes and the presence of a second distinct auditory patch, the *papilla amphibiorum* (both are unique to amphibians). The digestive system is simple. The digestive tube includes a large stomach and short intestines, typical of predators. Fat bodies (also called yellow bodies) store fat and are associated with the gonads in all amphibians. In anurans, the fat bodies form numerous finger-like projections which are larger and more pointed in males. These bodies serve as a source of nutrients for the gonads during the breeding period, after which they are in the smallest size. In males of the family Bufonidae, a growth of embryonic ovarian tissue, called Bidder's organ, is located between the fat bodies and the testicles. It is thought that it can develop in a functional ovary under certain conditions (Pancak-Roessler and Norris 1991).

After metamorphosed, anurans perform cutaneous (through the skin) and pulmonary respiration. The skin is highly vascularized and contributes significantly, but the lungs are always present. These are paired, conical sacs with a pulmonary membrane folded to form internal septa. The lung of anurans is structurally simple when compared to those from other tetrapods, lacking bronchiole, alveolus (like in mammalians and many reptiles) or air capillaries (like in birds). In the absence of ribs and a diaphragm, lung aeration is performed by buccal pumping. Amphibians have double circulation, but the hearth is divided into three chambers: two atriums and one ventricle.

Sexual Dimorphism

Sexual dimorphism is defined as phenotypic differences between conspecific males and females (Shine 1989). In anurans, it might be observed for many traits, such as coloration, skin texture and skin glands, vocalization, dermal ornamentations, vocal sacs (males), and breeding behavior, body size, and shape (Mesquita et al. 2004). Some differences persist throughout adult life, but others develop in response to gonadotropic hormones and therefore are present only during the active reproductive cycle. Some structures are used in courtship and others for holding the couple in an embrace during mating or oviposition (Duellman and Trueb 1994).

Sexual dimorphism description is very important in taxonomic studies, including body-size measurements, mainly because the female is usually larger than the male. However, interspecific variation in mean body size among closely related species is not clear unless sexual size dimorphism is taken into consideration. Larger body sizes in females might be an advantage for increased fecundity. Nevertheless, competition between males, female choice, parental care, and vocalization are the main drivers for equal or slightly larger individuals among males in species with aggressive behavior (Kupfer 2007; Han and Fu 2013).

In addition to body size, it is possible to distinguish between sexes externally by the nuptial excrescences (Fig. 5a, b) or hypertrophied forelimbs (Fig. 5c). Nuptial excrescences are associated with male-male combat or with amplexus. Hypertrophied forelimbs can be associated of holding the pair during in an embrace during mating or oviposition. Sometimes, the mature oocytes of adult females can be visually perceptible through the transparent tegument of the venter. Many other anurans exhibit sexual differences in skin texture, with either the male or female having rough or spiny skin that is not found in the other sex. These differences might function as tactile cues for sex recognition. The same is true for sexual differences in coloration, which is especially common in toads that are diurnally active.

Some frogs have glands of unknown function on various parts of the skin, and in many cases, these are sexually dimorphic or found only in one sex. Ventral glands are known to produce mucus secretions that glue the male to the female during amplexus in some rotund microhylids. In other frogs, these glands can either have the same function or produce pheromones that are transferred to the female during courtship or amplexus.

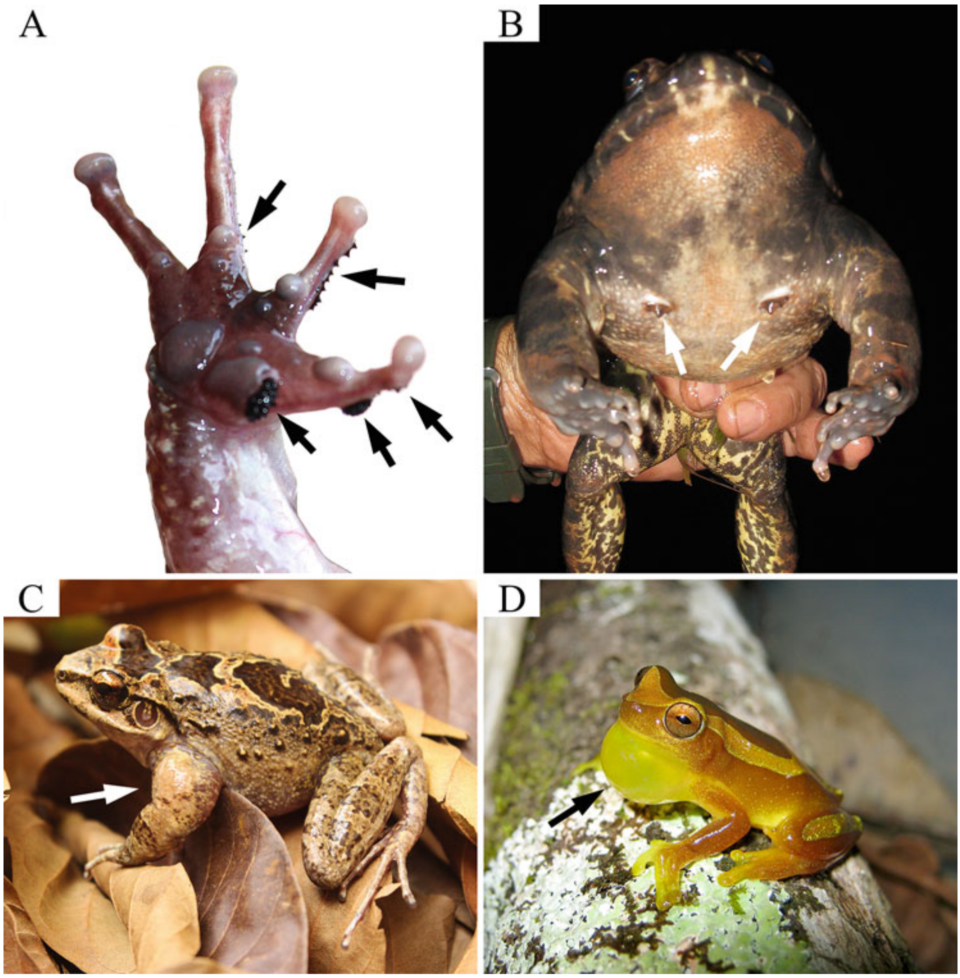
Calling is energetically expensive and requires suitable metabolic machinery to supply the muscles with large amounts of energy and oxygen. Vocalizations are usually emitted by males during the breeding season and the machinery necessary for its functions are: strong trunk muscles and large laryngeal apparatus in males than those of females; and vocal slits and sacs developed in males for most species (Fig. 5d).

When external sexual characters are absent or not visible, it is possible to determine sex and reproductive conditions through direct observation of the gonads. The bilaterally paired ovaries are ventromedial to the kidneys and suspended from the body wall by a pair of mesenteries. When enlarged with mature oocytes, the ovaries occupy much of the body cavity and may envelop other abdominal organs. Anurans oviducts are bilaterally paired and lie firmly held by peritoneum along the dorsal surface of the body cavity, extending from an adjacent position (usually ventral) to the lungs, posteriorly to the cloaca, lateral to each ovary. Reproductive males have testis that increase in size and become pigmented in some species during the breeding season. Such structures are attached ventrally to the kidneys by a membrane and usually are spheroid or ovoid small structures.

Evolution

Whether the Lissamphibia originated from the Lepospondyls or the Temnospondyls remains controversial, though a stronger case for the latter can be found in the literature. Likewise, the relationship between lissamphibian groups is also shrouded in controversy. Recent studies indicate a close relationship between Salientia and salamanders, with caecilians placed as an external group (Benton 2015). Perhaps the discovery of new salientian fossils will shed light on the emergence and evolution of this group.

The oldest known Salientia date from about 247 million years ago, in the lower Triassic: *Triadobatrachus* from Madagascar and *Czatkobatrachus* from Poland. Despite some obvious differences, these fossils closely resemble an extant anuran, especially regarding the flattened shape of the cranium. The first Salientia had a short tail, unlike the anuran fused postsacral vertebrae (urostyle). They also had a longer body, with up to 14 presacral vertebrae, and the limbs were shorter than that of extant anurans. In general, the overall skeletal morphology of extinct salientian shows an evolutionary path to the jumping habits found in anurans. After a large gap of about 60 million years since the occurrence of these two taxa in the fossil record, the Early Jurassic *Prosalirus* is the oldest known anuran, discovered in Arizona. This species had a vertebral column that resembles the one in modern anurans, though the exact number of presacral vertebrae is unknown. Nevertheless, the jumping habit is clearly already present. During the



Salientia Morphology, Fig. 5 Examples of sexual dimorphic characters present in males (pointed by arrows). (**a**) and (**b**) nuptial excrescences. (**c**) hypertrophied forelimb. (**d**) vocal sac

Jurassic period, anurans had a massive irradiation, and, by the end of this period, fossils attributed to several of the modern families are known. More on the evolution of the amphibians, including the Salientia, can be found in Carrol (2009) and Benton (2015).

Cross-References

▶ Adaptation
▶ Circulatory System
▶ Clade
▶ Color Change
▶ Digestive System
▶ Evolution
▶ Excretory System
▶ Fossil Record
▶ Integumental System
▶ Morphology
▶ Nervous System, The
▶ Ontogeny
▶ Phylogeny
▶ Reproduction
▶ Reproductive System
▶ Salientia Cognition
▶ Salientia Communication
▶ Salientia Diet

- ▶ Salientia Life History
- ▶ Salientia Locomotion
- ▶ Salientia Navigation
- ▶ Salientia Sensory Systems
- ▶ Secondary Sex Characteristics
- ▶ Sex Differences
- ▶ Sexual Dimorphism
- ▶ Skeletal System
- ▶ Specialization
- ▶ Taxa
- ▶ Vertebrate Nervous System
- ▶ Vertebrates (Chordata)

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